STRIKING SEXUAL DIMORPHISM IN *LINDERA SUBCORIACEA* (LAURACEAE)

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ABSTRACT

Male and female flower morphology is documented for Florida plants, augmenting the original floral analysis of this rare, dioecious species (*Lindera subcoriacea*). Sexual dimorphism is readily apparent; leaves on male plants are much larger than those on female plants. Leaf surfaces of the two sexes also contrast strongly in features of trichome size, epicuticular wax (abundance and pattern), and development of peristomatal rims. Such dimorphism has not been previously reported for the Lauraceae.

RESUMEN

Se documenta la morfología de flores masculinas y femeninas de *Lindera subcoriacea* en plantas de Florida, aumentando el análisis floral de esta especie rara y dioica. El dimorfismo sexual es muy aparente; las hojas de las plantas masculinas son mucho mayores que las de las plantas femeninas. Las superficies foliares de los dos sexos también contrastan fuertemente en cuanto a las características del tamaño de los tricomas, ceras epicuticulares (abundancia y patrón), y desarrollo de los bordes peristomáticos. Este dimorfismo no había sido citado previamente en las Lauraceae.

INTRODUCTION

Wofford described *Lindera subcoriacea*, the bog spice bush, in 1983. This species is now known to occur in at least eight states, ranging in coastal states from Louisiana to Florida north to Virginia (Bridges & Orzell 1989; Bryson et al. 1988; McCartney et al. 1989; Sorrie 1993). Although the range appears extensive, the plant is nowhere common. Most occurrences consist of one or a few plants. McCartney et al. (1989) signaled its possible presence in Florida by listing some peninsular populations as "*Lindera* affin. *subcoriacea*." Sorrie (1993) stated they have proven to be *L. benzoin* (L.) Blume, but these problematic peninsular plants need further study. Unequivocal *L. subcoriacea* was reported by Anderson (1995) from a population in the Florida panhandle.

More attention to the Florida panhandle plants is warranted because Wunderlin (1998) did not list the species for Florida, and additional field surveys since the initial report (Anderson 1995) have revealed new dimensions in the species' morphology.

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MATERIALS AND METHODS

The original plant upon which the Florida panhandle record was based (Anderson 1995) was destroyed by brush removal under the *Cliftonia* canopy along Metts Creek in Okaloosa County shortly after the collection was made. Intensive survey along Metts Creek and nine similarly nearly pristine clearwater streams in the general area (on Eglin Air Force Base) for additional bog spice bushes yielded a count of 12 plants (six of each sex, restricted to Metts Creek). James R. Burkhalter collected a sample (originally identified only as *Lindera*) from a presumably male shrub (sterile) on the campus of the University of West Florida in Escambia County. After being alerted to its identity, he searched the area thoroughly and reported (pers. comm.) that the plants were no longer extant as a result of habitat alteration.

Flowering materials were preserved in FPA (5 pts formalin, 5 pts proprionic acid, 90 pts 70% ethanol). Living plants were tagged at blooming time so that they could be more easily located later in the season. Samples with mature leaves were taken from only a few plants because of the species' rareness. Vouchers are at FSU unless otherwise noted. Leaf morphology (of the largest leaf per specimen) was studied from samples representing the geographical range of the species. Leaf samples were cleared in NaOH and stained in safranin for study of venation and trichomes. Other samples were sputter coated with gold palladium, and micrographs were taken on a Joel JSM-840 scanning microscope operated at 10KV.

RESULTS

Wofford (1983) reported the plants were up to 2 m tall (his original description was based solely on specimens from Mississippi and Louisiana as this species was not known to occur elsewhere at that time), whereas Sorrie (1993) said that in North Carolina the plants grew up to 4 m tall and were multistemmed. At Metts Creek (Florida) the blooming shrubs were 1.5–4.2 m tall with only 2–4 stems per clump. These deciduous shrubs bloom in mid-March (as they do in Mississippi) before leaf development.

Florida flowers of this dioecious species differ in several aspects from Wofford's description. Some of the differences in size may have arisen because his measurements came from restored (boiled) flowers, whereas mine came from preserved flowers. Wofford (1983) stated flower buds were ca. 2.5 mm wide and tepals were 2.2 by 1.8 mm. Further, in staminate flowers, stamens were 2.5 mm long, and the pistillodium was 1.2 mm long (Wofford 1983). In our plants, staminate flowers were generally larger (2.8–3.2 mm long by 3.8–4.5 mm wide at anthesis); outer tepals were 2.4–2.8 by 1.8–2.0 mm, whereas inner tepals were slightly smaller (2.2–2.5 by 1.5–1.7 mm). The nine stamens were 2.7–2.9 mm long; the innermost series of three had a

pair of stalked (1 mm) glandular outgrowths. The glandular heads were 0.8 mm wide and had 3–4 irregular lobes.

The original description (Wofford 1983) stated pistillate flowers were on pedicels 1.5 mm long, with tepals slightly smaller that those of staminate flowers, and stamens (staminodes) variously developed, often reduced to glands. The style was 1 mm long, and the ovary elliptic and 1.0 by 0.6 mm. In our plants, pistillate flowers were on pedicels 1.5–2.5 mm long. Flowers were 1.8–2.2 mm long (style excluded) by 2.2–2.6 mm wide. The outer tepals were 2.0–2.2 by 1.1–1.4 mm, and the inner tepals were 2.0 by 1.4–1.5 mm (relatively wider than the outer tepals). The six outer staminodes (in two series) were reduced to naked filaments 1.4 mm long (no vestige of anthers), whereas the three innermost staminodes (also filaments 1.4 mm long) had a pair of flattened, stalked glands fused basally to the filament. The glands differed from those of the staminate flowers in that the heads (0.8 mm wide) were broadly cordate and lacked irregular lobes. Styles were 1.4–1.8 mm long and often curved. The elliptic ovaries were 1.6–1.8 mm long by 0.9–1.0 mm wide. Mature fruits were scarlet, elliptical, and 10 mm by 6 mm.

Wofford and Sorrie both gave the same range of 4–7.5 cm long by 2–3.5 cm wide for leaves of *L. subcoriacea* (Fig. 1). Leaves of female shrubs in the Metts Creek population fall in that size range; the largest leaves per sample (usually the penultimate on any given branch) measured 5.6–6.8 cm long by 2.4–2.8 cm wide (Figs. 2–4). This dioecious species exhibits sexual dimorphism, however; leaves on the male shrubs are 9.0–10.5 cm long by 3.5–4.6 cm wide (Figs. 5–7). The ranges in leaf size of the two sexes are almost completely nonoverlapping, if one discounts the very small broadly obovate leaves that occur basally on the branches (they are 1–2 cm long on female shrubs and 3.3–5 cm long on male shrubs). Incidentally, female plants of *L. benzoin* var. *pubescens* from Florida have leaves larger than any seen in *L. subcoriacea*.

Mature leaves were dark green adaxially, whereas the abaxial (undersurface) area was generally pale, grayish, glaucescent, and moderately appressed pubescent. Venation is brochidodromous (Figs. 1–7; Hickey 1979), and the areoles are well developed. Trichomes were nonglandular and unicellular (Figs. 8–9), as is typical for the Lauraceae (Metcalfe & Chalk 1979). Average trichome length on leaves of four Florida female shrubs ranged from 0.19 to 0.22 mm long [and 0.23 on *Wofford 82-121* (TENN), an isotype], whereas trichomes on Florida male shrubs averaged 0.29–0.32 mm long. The longer trichomes on male shrubs also appear to be somewhat thicker than those on female shrubs (Figs. 11–13).

Stained, partially cleared leaves showed the epidermal cells were thin-walled; stomatal guard cells were 24–26 μm long, and the stomata were paracytic (similar to those of fossil forms of *Lindera* illustrated by Bandulska

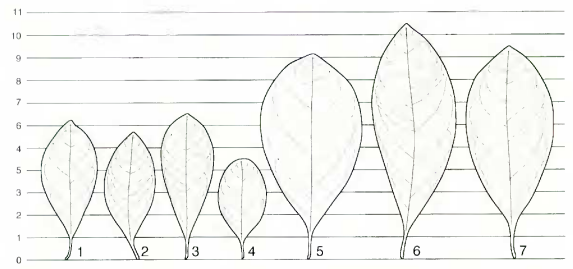

FIG. 1–7. Comparative size (scale in cm) and shape of leaves (largest per branch) in *Lindera subcoriacea*, showing brochidodromous venation (i.e., secondary veins joined together in a series of prominent arches). Fig. 1. Leaf from female plant from George Co., MS, *Wofford 82-121* (A, holotype). Fig. 2–4. Leaves from female plants from Okaloosa Co., FL. Fig. 2. *Anderson 14452*. Fig. 3. *Anderson 14920*. Fig. 4. *Anderson 13851*. Fig. 5–6. Leaves from male plants from Okaloosa Co., FL. Fig. 5. *Anderson 14922*. Fig. 6. *Anderson 14921*. Fig. 7. Leaf from male plant from Escambia Co., FL, *Burkhalter 5658*.

1926). The two subsidiary cells tended to be unequal in size on female leaves; one cell was somewhat rectangular and lay parallel to the guard cell, whereas the other subsidiary cell was more triangular in outline. Conversely, stomata on male leaves had more evenly shaped, triangular subsidiary cells.

The grayish appearance of the leaf undersurface was due to wax accumulation more than to indumentum (Figs. 10–16) as demonstrated by scanning electron microscopy (SEM). The thick layer of cuticular wax obscures epidermal cell outlines. A papillose abaxial leaf surface is characteristic of the Lauraceae (Metcalfe &Chalk 1979). The stomata on *L. subcoriacea* leaves are sunken and surrounded by prominent stomatal rims; peristomatal rims are also evident—see Wilkinson (1979) for overview of these stomatal structures. Stomatal rims and peristomatal rims may prove to be frequent among woody taxa that have relatively firm (subcoriaceous) leaves in the southeastern United States flora; elaborate rims have also been reported for *Gordonia* (Anderson 1983) and *Sideroxylon* (Anderson 1996).

Sexual dimorphism is also evident at the micromorphological level. Leaves of female plants have extensive epicuticular wax papillae over the epidermal cells and the massive peristomatal rims (Figs. 10–12, 14–15). Leaves of male plants have scattered epicuticular flecks of wax that do not hide the cuticle, and peristomatal rims are not massive, but are present as 1–3 ridges lying parallel to the long axis of the stomatal rim (Figs. 13, 16).

Unisexual flowers are, by definition, dimorphic, but in *L. subcoriacea* the

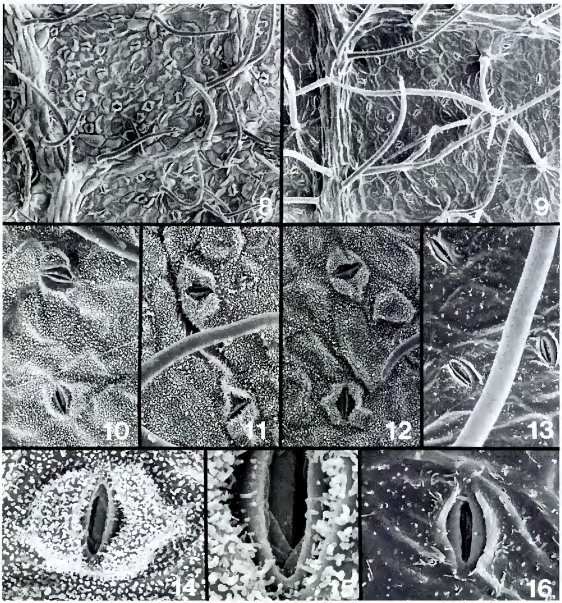

FIG. 8–16. Electron micrographs of leaf surfaces in *Lindera subcoriacea*. Figs. 8–9. Venation and trichomes, × = 100 . Fig. 10–13. Leaf surfaces showing cuticle and stomatal features, × = 500 . Fig. 8. Leaf from female plant, *Anderson 14452*. Fig. 9. Leaf from male plant, *Anderson 14921* showing trichomes slightly longer and thicker than those on female leaf (Fig. 8). Fig. 10. Female from George Co., MS, *Wofford 82-121* (TENN, isotype). Fig. 11. Female from Hoke Co., NC, *Carter s.n.* Figs. 12. Female from Okaloosa Co., FL, *Anderson 14452*, showing nearly continuous layer of epicuticular papillae and large peristomatal rims (as in Fig. 10–11). Fig. 13. Male from Okaloosa Co., FL, *Anderson 14921* showing scattered epicuticular flecks, reduced development of peristomatal rims, and thicker trichomes (than female leaves, Fig. 10–12). Fig. 14. Leaf surfaces of *Anderson 14452* (female plant) showing massive peristomatal rims covered with epicuticlar papillae with stomatal rim barely visible, × = 1500. Fig. 15. Portion of Fig. 14 showing detail of epicuticular papillae and part of stomatal rim with the peristomatal rim, × = 3500. Fig. 16. Leaf surface of *Anderson 14921* (male plant) showing sparse eipcuticular flecks of wax and partial development of peristomatal rim (forming brackets or ridges parallel to the stomatal rim), × = 1500.

dimorphism extends to nonsexual parts of the flower with the different shapes of glandular heads on staminodes. Sexual dimorphism in the Florida plants is expressed vegetatively in leaf size, trichome length, epicuticular wax patterns, stomata (subsidiary cells), and peristomatal rim development. Vegetative sexual dimorphism has been reported for *L. benzoin* (Cipollini & Whigham 1994), in which leaves on male shrubs averaged 1.3 times longer than those on female shrubs. In *L. subcoriacea* the dimorphism is more pronounced; male leaves average 1.7 times longer than those on female shrubs. Apparently, vegetative sexual dimorphism at the microscopic level has not been previously reported for *Lindera* or any other dioecious members of the Lauraceae (Wood 1958; van der Werff 1991).

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